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THE FERN GENUS *POLYSTICHUM* David S. Barrington²
(DRYOPTERIDACEAE) IN
COSTA RICA¹

ABSTRACT

The fern genus *Polystichum* Roth (Dryopteridaceae) remains one of the most difficult genera taxonomically. In this work, I provide an identification guide to the Costa Rican *Polystichum* species in the context of an evaluation of characters and evolution in the genus in the Neotropics. Key characters are those of petiole and pinna-rachis scales, ultimate segment shape, and indusium. There are 12 species in the country, of which three are allopolyploids (*P. lilianiae* Barrington, *P. orbiculatum* (Desv.) J. Rémy & Fée, and *P. talamancanum* Barrington). The species' distributions vary: while five are widespread in Tropical America, two are at the southern end of their range (*P. alfaroi* (Christ) Barrington and *P. speciosissimum* (A. Braun ex Kunze) R. M. Tryon & A. F. Tryon), and two are at the northern end (*P. dubium* (H. Karst.) Diels and *P. nudicaule* Rosenst.). Three are confined to Costa Rica and Panama: *P. concinnum* Lellinger ex Barrington and the allopolyploids *P. lilianiae* and *P. talamancanum*. Essentially a denizen of wetter montane regions throughout the world, the genus in Costa Rica is most prominent in higher-elevation rainforests and to a lesser extent in the páramos of the Cerro de Talamanca. The names *P. aculeatum* var. *flavidum* Rosenst., *P. nudicaule* Rosenst., and *P. opacum* Rosenst. are lectotypified.

RESUMEN

Polystichum Roth (Dryopteridaceae) es un género de helechos con dificultades taxonómicas que complican la identificación de sus especies. En este trabajo, presento una clave de identificación taxonómica para las especies de *Polystichum* en Costa Rica analizando diferentes caracteres morfológicos y la evolución del género en el Neotrópico. Los caracteres más importantes pertenecen a las escamas de peciolo y raquis de la pinna, forma de los últimos segmentos, e indusio. En el país se encuentran 12 especies, incluyendo tres poliploides. La distribución de las especies es variable: cinco se ubican en toda la América tropical, dos se extienden en el borde sur y dos en el borde norte de estas áreas tropicales, y tres (incluyendo dos allopoliploides) se limitan a Costa Rica y Panamá. *Polystichum* es un componente común de las selvas más húmedas de montañas en todo el mundo, en Costa Rica el género se encuentra típicamente en elevaciones altas, en selvas lluviosas y en páramos del Cerro de Talamanca. Los nombres *P. aculeatum* var. *flavidum* Rosenst., *P. nudicaule* Rosenst., y *P. opacum* Rosenst. son lectotipificados.

Key words: Costa Rica, Dryopteridaceae, ferns, *Polystichum*.

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Among the prominent ferns in the high-montane forests and páramos of Costa Rica are species of the terrestrial fern genus *Polystichum* Roth, known in English as “holly ferns.” *Polystichum*, one of the 10 largest fern genera (data from Smith et al. [2006]), is most diverse in subtropical regions of both the New World and Old World, but it is also diverse in tropical montane regions. In addition, the genus can be found in the alpine zone—in the Sino-Himalayan Region (sensu Takhtajan, 1986), in New Guinea, and in the Neotropics. About one third of the species in the genus is found in the American tropics, where there are three centers of diversity: the Greater Antilles (31 species [Mickel, 1997]), Mexico and Guatemala (18 species [Stolze, 1981; Mickel & Smith, 2004]), and the North and Central Andes (29 species [Kessler et al., 2005; McHenry & Barrington, unpublished]).

The taxonomy of the genus *Polystichum* remains unresolved in spite of substantial recent study (Roux, 2000; Little & Barrington, 2003; Driscoll & Barrington, 2007; Lu et al., 2007; Li et al., 2008). It is possible to delineate a monophyletic genus *Polystichum* as long as *Cyrtomium* C. Presl s. str. is excluded; the species allied to *C. balansae* (Christ) C. Chr. are polystichums (Li et al., 2008). However, the subgeneric taxonomy is in chaos because (1) the key works on sections, by Daigobo (1972) and Roux (2000), are not based on a critical review of world morphology or genetic variation; (2) sections have been typified by allopolyploids (e.g., *Polystichum* sect. *Aculeata* Christ and *Polystichum* sect. *Lasiopolystichum* Daigobo); and (3) morphological convergence is rampant in the genus. In fact, given our present primitive understanding of phylogeny and character variation in the genus, it would be folly to attempt a subgeneric classification.

Costa Rica lies in a unique geographic position in the American tropics, between the high-montane regions of Mexico and Guatemala to the northwest and the northern Andes to the east and south. The provenance of the higher-elevation fern diversity in Costa Rica is a mix of species with two geographic patterns: species also found in the Andes and species that are common to the north in southern Mexico and Guatemala (Barrington, 2005). There is a tendency in the Costa Rican ferns for the páramo species to extend to the south and the montane-forest species to extend to the north (Barrington, 2005). *Polystichum* in Costa Rica fits these general patterns, but with some notable exceptions.

Neotropical *Polystichum* is monophyletic, based on a molecular phylogenetic analysis of a sample of nine species included in a recent world phylogeny

(Driscoll & Barrington, 2007). In this analysis, the polystichums found in Costa Rica fall into three groups. *Polystichum speciosissimum* (A. Braun ex Kunze) R. M. Tryon & A. F. Tryon is sister to all the other species. The remaining species fall into two monophyletic lineages. The first is an indusiate alliance (which I call the Mayan clade) including species endemic to Central America. The second is an exindusiate lineage (the Andean clade) including species endemic to the Central Andes.

Identification of *Polystichum* species in the field and in the herbarium remains an extraordinary challenge, and herbaria continue to have high levels of misidentification in the genus. Forty years of fieldwork in Costa Rica have yielded a diversity of insights into the delimitation, habitat preference, and geographic provenance of the species in the country. In this paper, I seek to synthesize these data into a treatment of the Costa Rican species that will (1) serve as an identification guide, (2) provide insights into the natural history and evolutionary biology of these elegant and confusing plants, and (3) point the way to addressing the remaining problems.

MATERIALS AND METHODS

Herbarium materials from A, AAU, BM, CR, DS, E, GH, K, L, MO, NA, NY, P, UC, US, and VT formed the basis for this study. The materials at VT (for which there are often duplicates at CR) are the result of 21 excursions to Costa Rica between 1970 and 2011. I have made numerous observations in the field in Costa Rica that provide insight into the diversity and ecology of Costa Rican *Polystichum* species. An array of genetic analyses of Costa Rican polystichums from my lab (e.g., Barrington, 1990, 2003; Little & Barrington, 2003; Driscoll & Barrington, 2007) informs the morphological work reported here.

GENERAL CONSIDERATIONS

THE NATURE OF VARIATION IN COSTA RICAN *POLYSTICHUM*

Four kinds of problems complicate the naming of *Polystichum* species: (1) phenotypic variation, (2) changes associated with increased size over an individual's lifespan, (3) challenges presented by indument characters, and (4) hybridization. However, paucity of characters that are stable within species and labile between species is not a problem. There is a wealth of morphological characters to choose from (Little & Barrington, 2003), and close analysis yields characters with real power to distinguish even closely allied species (e.g., Barrington, 2003).

Phenotypic variation is rampant: characters such as petiole length, petiole color, and the curvature of pinnule margins are all labile in relation to variation in light levels. For instance, plants from the highly insolated habitats above treeline in the Cerro de la Muerte have much shorter petioles and much more recurved segments than genetically identical plants from the small shaded stream banks nearby. Unfortunately, these characters are prominent and have often been used as the basis for describing species in *Polystichum*.

Variation with size is also common. For instance, though valuable in distinguishing species, petiole scale color varies with size of leaf and thus presumably with age of the individual among fertile plants of *Polystichum*. The key variable is value in the sense of the Munsell color solid (e.g., Munsell, 1966); larger, older plants have darker scales than younger, smaller plants of the same species. Shape also varies with size: it is common for small fertile leaves of a species to differ in shape from larger leaves, especially in overall length:width ratio and in the length of the basal pinnae. Leaf dissection presents similar patterns: some species—notably *P. alfaroi* (Christ) Barrington, *P. hartwegii* (Klotzsch) Hieron., and *P. platyphyllum* (Willd.) C. Presl—are prone to increase in lamina dissection with increase in plant size.

Though critical to species identification in *Polystichum*, indument presents several challenging problems; most important is positional equivalence. An indument character must be scored from the same position on the same organ across the plants of the study set to ensure the homology inherent in the character. For instance, although the shape of pinna-rachis scales is one of the most powerful characters for distinguishing *Polystichum* species, the variation in scales lying in different positions on the pinna-rachis (base of the pinnules vs. between the pinnule attachments) can obscure the stable character states that divide species. Petiole scales present another problem of position. Since the scales at the base of the petiole are routinely different from those above the base, distinguishing the basalmost scales from the more distal is critical. However, collections with leaves but no stems often do not have the material to ensure that the most proximal portion of the petiole was collected. To make matters worse, some of the most useful indument characters in *Polystichum* are vulnerable to loss in herbaria. Notable are the features of the cilia on the edges of petiole scales, which are powerful characters for distinguishing species. The more delicate cilia are especially vulnerable to being worn off during collection or

routine handling of herbarium specimens, making the characters unscorable.

Hybridization and polyploidy are common in Costa Rican *Polystichum* (Barrington, 1990, 2003). Three Costa Rican polystichums are allopolyploids, and four hybrids have been documented. Emblematic of the problems presented by hybrids in Costa Rica is the backcross hybrid between *P. talamancanum* Barrington and *P. concinnum* Lellinger ex Barrington, which is common in mixed populations with its tetraploid parent in disturbed terrain above treeline in the Cerro de la Muerte. The morphological discontinuity between the two progenitors is largely obscured by the backcross hybrid.

DIVERSITY, ECOLOGY, AND BIOGEOGRAPHY

The genus *Polystichum* in Costa Rica comprises 12 species; nine of the 12 are diploid. Ecologically, two of the nine diploids (*P. nudicaule* Rosent. and *P. speciosissimum*) are characteristic páramo species growing above 3000 m. Five other diploid species are found in forests. These include two montane rain-forest species (forest classification follows Holdridge [1987] throughout), one of which has among the largest leaves in the genus (*P. concinnum*), while the other is a diminutive species with unusually thin rhizomes for the genus (*P. turrialbae* Christ). The remaining three are to be found in premontane moist to wet forests (*P. alfaroi*, *P. muricatum* (L.) Fée, and *P. hartwegii*). Finally, two diploids (*P. platyphyllum* and *P. dubium* (H. Karst.) Diels) are characteristic of stream banks and earthen banks in premontane wet and rainforests in Costa Rica. The diploids from the forests are indusiate; those from páramo and stream bank are exindusiate. Biogeographically, the forest diploids are related to indusiate species endemic to Mexico and Central America, whereas most of the páramo and stream bank species are related to exindusiate species confined to the Andes. The single exception is *P. speciosissimum*, a páramo species disjunct from Mexico and Guatemala. Among the diploids, only the montane rainforest *P. concinnum* is endemic to the Talamanca massif; all others are either more widely distributed to the north (*P. alfaroi*, *P. speciosissimum*) or to the south (*P. dubium*, *P. nudicaule*) or are broadly distributed in the American tropics (*P. hartwegii*, *P. muricatum*, *P. platyphyllum*, *P. turrialbae*).

The three remaining species in Costa Rica are allotetraploids, all from high-montane forests and páramos. Two are endemic: *Polystichum lilianiae* Barrington (high-montane) combines the heritage of the widespread *P. turrialbae* with an unknown second species, whereas *P. talamancanum* (páramo) com-

bines the heritage of the endemic *P. concinnum* with an unknown second progenitor. The remaining tetraploid is *P. orbiculatum* (Desv.) J. Rémy & Fée (páramo). A prominent member of the central and northern Andean páramo communities (Barrington et al., 1986), *P. orbiculatum* is found north of Costa Rica only on Volcán Tacaná at the border between Mexico and Guatemala (Smith, 1981). *Polystichum orbiculatum* does not yet have identified living progenitors, but one of its progenitors is also the unknown second progenitor of *P. talamancanum* (Barrington, 1990). Small spores encountered in northern Andes individuals suggest that an undetected diploid progenitor may be there (Barrington et al., 1986).

Polystichum is largely a montane genus throughout the world. In Costa Rica the genus is only found in the mountains. It becomes ecologically prominent at upper elevations on the Cordillera de Talamanca and the Cordillera Central (the volcanoes). Few records exist from the Cordillera de Tilarán and the Cordillera de Guanacaste. The small mountain ranges in the Central Valley (the Cerro de la Carpintera southwest of Cartago and the Cerros de Escazú south of San José) also host polystichums, and there are historical (lost) stations in the Central Valley itself, especially along the rivers. Three species of Costa Rican polystichums are of conservation concern; all are from lower montane and premontane forests under substantial development pressure. *Polystichum dubium*, for which a single Costa Rican station is known to be extant, appears to be most critical. Also of concern are *P. platyphyllum* and *P. hartwegii*, both of which are represented by few modern collections from the country.

TAXONOMIC TREATMENT

Polystichum Roth, Tent. Fl. Germ. 3(1): 31, 69. 1799, nom. cons. TYPE: *Polystichum lonchitis* (L.) Roth, Tent. Fl. Germ. 3(1): 31, 69. June–Sep. 1799.

Plants terrestrial; rhizomes erect or ascending, rarely branched; indument entirely of scales including uniseriate scales (sensu Moran, 1987). Leaves of fertile individuals monomorphic, clustered at the stem apex; petioles adaxially sulcate, with more than 2 leaf traces, edges of the petiole scales usually with cilia (except *Polystichum muricatum*) but without a histologically differentiated margin (except *P. alfaroi*); blades usually 2-pinnate (rarely 1-pinnate or 2-pinnate pinnatisect), gradually reduced at the apex (not conform or subconform); ultimate segments spinulose or at least dentate-mucronate; veins free

and forked (occasionally anastomosing without included veinlets in *P. dubium*), extending to the margin, lacking hydathodes; sori round, abaxial or terminal on the veins; indusiate or not, the indusia true (abaxial on the receptacle) and peltate or false (a modified segment edge, only in *P. speciosissimum*).

TAXONOMIC KEY TO THE SPECIES OF COSTA RICAN
POLYSTICHUM

- 1a. Blades once-pinnate (indusia absent) ... 3. *P. dubium*
- 1b. Blades twice-pinnate to twice-pinnate pinnatisect 2
- 2a. Indusia absent (but present in a few sori on some individuals of *P. talamancanum*) 3
- 3a. Bulbil present at base of pinna near leaf apex, pinnules flat, below 2000 m 9. *P. platyphyllum*
- 3b. Bulbil absent, pinnules strongly recurved except in deep shade, above 2800 m 4
- 4a. Pinnules deeply pinnatisect throughout, basal petiole scales orange 10. *P. speciosissimum*
- 4b. Pinnules crenate (sometimes basally pinnatisect in *P. orbiculatum*), basal petiole scales various colors, but not orange 5
- 5a. Basal petiole scales atropurpureous or fuscous; pinnae, if ascendant, more than 6 times as long as wide 6
- 6a. Pinnae attenuate, the basal pinnae as long as or longer than the next distal, pinnules oblique to the pinna-rachis 7. *P. nudicaule*
- 6b. Pinnae acuminate, pinnules attached at right angles to the pinna-rachis 11. *P. talamancanum*
- 5b. Basal petiole scales rufous; pinnae both ascendant and up to 6 times as long as wide 8. *P. orbiculatum*
- 2b. Indusia present 7
- 7a. Small plants (leaves to ca. 50 cm) with small (up to 1 cm), stramineous basal petiole scales (fulvous to fuscous central stripe present in *P. lilianiae*), abundant very short cilia on the petiole scales, and broad-based pinna-rachis scales 8
- 8a. Pinnae acuminate; basal pinnae not the longest; pinnules of medial pinnae attached at right angles to pinna-rachis; petiole-base scales uniformly pale or with a weakly defined brown stripe at the center 12. *P. turrialbae*
- 8b. Pinnae attenuate; basal pinnae the longest; pinnules of medial pinnae attached at about a 60° angle to pinna-rachis; petiole-base scales with a sharply defined brown stripe at the center 5. *P. lilianiae*
- 7b. Medium to large plants (leaves 50 cm or more) with larger (1 cm or more), fuscous to rufous basal petiole scales (*P. muricatum* and *P. hartwegii* may have fuscous basal petiole scales with a narrow fulvous edge); petiole-scale cilia various but not abundant and short; pinna-rachis scales various.
- 9a. Indusia small (ca. 0.3 mm diam.), petiole-scale cilia absent 6. *P. muricatum*
- 9b. Indusia ca. 0.5 mm to over 1 mm diam., petiole-scale cilia present 10
- 10a. Indusia over 1 mm diam.; pinnae ca. 3 cm wide; pinna-rachis scales filiform 4. *P. hartwegii*
- 10b. Indusia 0.5–0.8 mm diam.; pinnae 1.5–2 cm wide; pinna-rachis scales various 11.

- 11a. Pinna-rachis scales lanceolate; basal petiole scales narrow (ca. 6:1), conform; basal acroscopic pinnules of medial pinnae often shorter than the next distal pinnule 2. *P. concinnum*
11b. Pinna-rachis scales filiform; basal petiole scales broad (ca. 4:1), marginate; basal acroscopic pinnules of medial pinnae longer than the next distal pinnule 1. *P. alfaroi*

1. *Polystichum alfaroi* (Christ) Barrington, Rhodora 94: 328. 1992. Basionym: *Polystichum aculeatum* var. *alfaroi* Christ, Bull. Herb. Boissier, sér. 2, 4: 963. 1904. TYPE: Costa Rica. San José: Alajuelito, 1300 m, Mar. 1902, A. Alfaro 16471 (holotype, P not seen; isotype, US!). Figure 2.

Polystichum aculeatum var. *flavidum* Rosenst., Repert. Sp. Nov. Regni Veg. 22: 9. 1925. TYPE: Costa Rica. Cartago: Cartago, 1400 m, A. C. Brade 555 (lectotype, designated here, B not seen; isoelectotype, UC-405822!).

Rhizome erect, reaching ca. 5 cm diam. Fronds typically 60–80 cm, spreading; petiole scales ca. 1.5 cm, lanceolate, marginate, rufous, petiole-scale cilia short and delicate. Laminae 2 to 3 times as long as wide, acuminate, 2-pinnate and crenate to 2-pinnate pinnatisect, without a bulbil; pinnae attenuate, ca. 8 times as long as wide, attached at right angles to the rachis, the basal pinnae often the longest; pinna-rachis scales filiform (or narrow-lanceolate), rufous; pinnules flat, obliquely attached throughout, the auricle weakly developed, the apex acute, spinules weak (developed only at apex and auricle), the basal acroscopic pinnule of the medial pinnae longer than the adjacent pinnule. Indusia ca. 0.6 mm in diam.

Discussion. *Polystichum alfaroi* is a large fern with notably lustrous upper leaf surfaces; the long pinnules with acute tips help to identify the species. The marginate petiole scales are unique among Costa Rican polystichums. The species honors Anastasio Alfaro (1865–1961), one of the prominent naturalists of the active scientific community in San José in the late 19th and early 20th centuries and long director of the Museo Nacional de Costa Rica.

Polystichum alfaroi occurs from 1100 to 2200 m on the Cordillera de Guanacaste, Cordillera Central, Cerros de la Carpintera, and the Cordillera de Talamanca including the Cerros de Escazú, mostly on leeward (southwest-facing) slopes. This distribution is apparently driven by *P. alfaroi*'s unique habitat among Costa Rican polystichums, the moist premontane forest, where it is a prominent fern (Barrington, 1992). This vegetation zone has been extensively cleared for agriculture, so the species is hard to find. The problem is epitomized by the type locality, now lost to urbanization in the Valle Central.

Geographically, *Polystichum alfaroi* presents a striking disjunct distribution, with the other populations in southernmost Mexico (Chiapas), Guatemala, and El Salvador (Barrington, 1992). *Polystichum alfaroi* is diploid, based on isozyme banding pattern (Barrington, 1992). It lies in the Mayan clade, based on molecular phylogenetic work (Driscoll & Barrington, 2007).

Remaining syntype material includes two collections from the Cerros de la Carpintera (A. C. Brade 26, Brade 26a).

Selected specimens examined. COSTA RICA. **Cartago:** mtns. above Tres Ríos, E. Scamman 7945 (GH). **Guanacaste:** Monteverde, Bajo del Tigre Reserve, D. S. Barrington 2354 (VT). **San José:** La Carpintera, R. Torres R. 170 (CR); Río Tiribi, Hda. La Verbena Alajuelita, O. Jiménez L. 395 (CR, US).

2. *Polystichum concinnum* Lellinger ex Barrington, Ann. Missouri Bot. Gard. 76: 367, fig. 1. 1989. TYPE: Costa Rica. San José: Villa Mills S of the Pan American Hwy. ca. 1 km E of Hotel La Georgina, ca. 3100 m, D. S. Barrington 694 (holotype, GH!; isotype, VT!). Figure 1.

Rhizome erect, ca. 28 cm diam. Fronds to at least 1.2 m, spreading; petiole scales ca. 3 cm, narrow-lanceolate, conform, fuscous, petiole-scale cilia long and delicate below, short and stiff above. Laminae ca. 4 times as long as wide, acuminate, 2-pinnate and crenate, without a bulbil; pinnae attenuate, ca. 8 times as long as wide, attached at right angles to the rachis, the basal pinnae shorter than the next distal; pinna-rachis scales lanceolate, fulvous; pinnules flat, attached at right angles throughout, the auricle weakly developed, the apex acute, spinules weak (developed only at apex and auricle), the basal acroscopic pinnule of the medial pinnae often shorter than the adjacent pinnule. Indusia ca. 0.6 mm in diam.

Discussion. *Polystichum concinnum* is the largest of the Costa Rican polystichums. The very dark, narrow-lanceolate petiole scales are shared only with the ordinarily exindusiate *P. talamancanum*. The species is unique among Costa Rica polystichums in often having the basal pinnules of the pinnae shorter than the rest. Young mature individuals from open sites, such as road cuts along the Pan American Highway, are superficially quite different from the large old-forest plants of this species; the lamina is broader, the pinnules are entire, and the lamina color is more yellow-green. These plants are not genetically distinct in their isozyme profiles (Barrington, unpublished). Where *P. concinnum* grows near highways, it commonly has sori transformed into globose galls up to 8 mm in diameter that bear untransformed

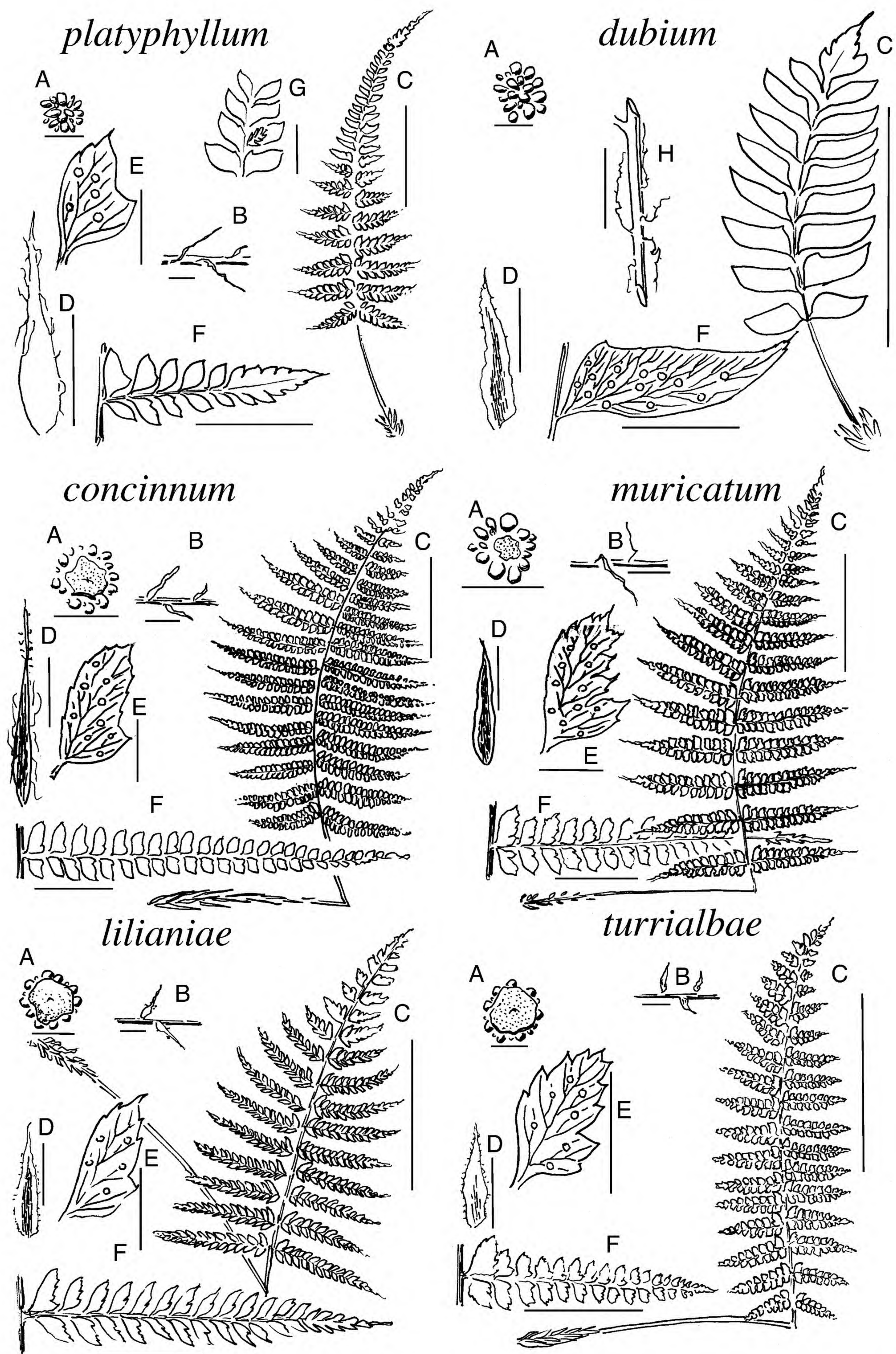


Figure 1. The Costa Rican species of *Polystichum*. *P. platyphyllum* (Willd.) C. Presl. A–G drawn from D. S. Barrington 1973 (VT). *P. dubium* (H. Karst.) Diels. A, C, D, H, F drawn from A. Rojas & P. L. Pacheco 5075 (VT). *P. concinnum* Lellinger ex Barrington. A–F drawn from D. S. Barrington 724 (VT). *P. muricatum* (L.) Fée. A–F drawn from D. S. Barrington 1240 (VT). *P. lilianiae* Barrington. A–F drawn from D. S. Barrington 1926 (CR). *P. turrialbae* Christ. A–F drawn from D. S. Barrington 2050 (VT). —A. Sorus; scale bar = 1 mm. —B. Pinna-rachis scales; scale bar = 1 mm. —C. Leaf; scale bar = 15 cm. —D. Basal petiole scale; scale bar = 5 mm. —E. Medial pinnule; scale bar = 5 mm. —F. Medial pinna; scale bar = 3 cm. —G. Lamina near apex; scale bar = 1 cm. —H. Rachis scales; scale bar = 2 mm.

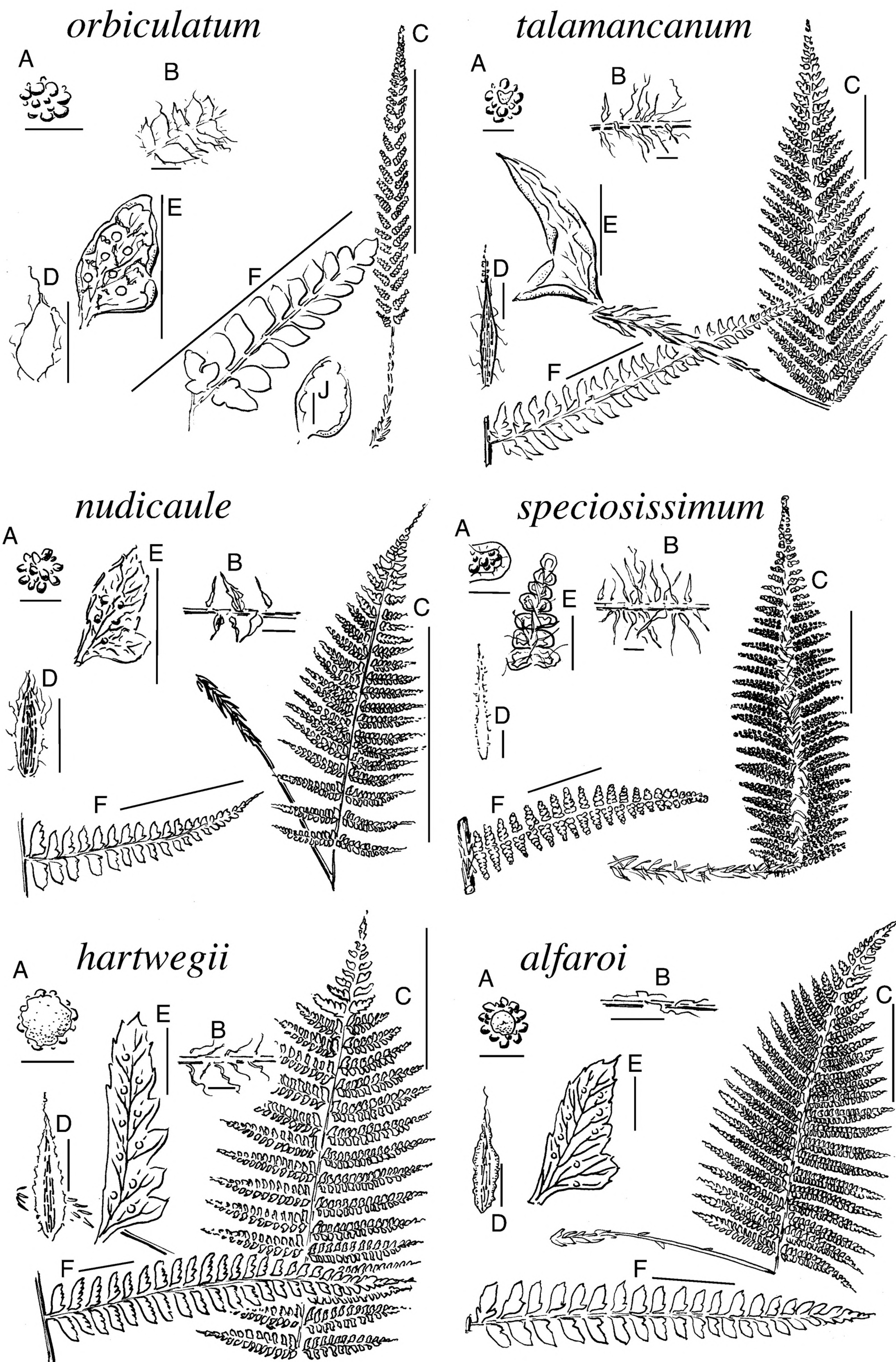


Figure 2. The Costa Rican species of *Polystichum*. *P. alfaroi* (Christ) Barrington. A–F drawn from D. S. Barrington 1213, 1242 (VT). *P. hartwegii* (Klotzsch) Hieron. A–F drawn from C. Hamilton & H. Stockwell 3615A (VT). *P. nudicaule* Rosenst. A–F drawn from D. S. Barrington 1277, 1555 (VT). *P. orbiculatum* (Desv.) J. Rémy & Fée. A–F, J drawn from D. S. Barrington 1284 (VT). *P. speciosissimum* (A. Braun ex Kunze) R. M. Tryon & A. F. Tryon. A–F drawn from D. S. Barrington 977 (VT). *P. talamancanum* Barrington. A–F drawn from G. Davidse 25034 (VT). —A. Sorus; scale bar = 1 mm. —B. Pinna-rachis scales; scale bar = 1 mm. —C. Leaf; scale bar = 15 cm. —D. Basal petiole scale; scale bar = 5 mm. —E. Medial pinnule; scale bar = 5 mm. —F. Medial pinna; scale bar = 3 cm. —J. Near-apical pinnule; scale bar = 1 mm.

sporangia and true hairs on the surface. The hairs are notable in that hairs are generally not found on tropical American *Polystichum* species, suggesting the release of a silenced hair-production developmental pathway by the gall formation process.

Polystichum concinnum occurs from 1600 to 3400 m in forests and disturbed terrain on the Cordillera Central and the Cordillera de Talamanca as far south as Chiriquí Province in Panama. It is the only large *Polystichum* in the oak-dominated montane rain-forests of the Sierra Talamanca, where it is common. In these forests, *P. concinnum* prefers sites that suggest a history of disturbance within the intact forest, such as along stream courses and on earthen banks. The species is especially common in the secondary forest that has grown up on sites disturbed by the construction of roads at higher elevations. *Polystichum concinnum* has an unusually broad elevational distribution. Plants I encountered at ca. 1600 m outside of San Gerardo, at the base of the main foot trail to Cerro Chirripó in disturbed terrain cleared from wet premontane forest, are typical *P. concinnum* both morphologically and genetically. *Polystichum concinnum* also extends above treeline (reaching at least 3400 m) on the Sierra Talamanca in open disturbed sites such as borrow-pit excavations.

Polystichum concinnum is endemic to the Cordillera Central and the Cordillera de Talamanca in Costa Rica and Panama. It is diploid based on meiotic chromosome counts (Barrington, 1990). Morphologically, it most closely resembles Mexican species such as *P. distans* E. Fourn.

Selected specimens examined. COSTA RICA. **Cartago:** Villa Mills, below but in sight of La Georgina, *D. S. Barrington* 686 (CR). **Heredia:** 1.7 km NNE of Porrosatí, on Río Ciruelas, 10°06'N, 84°05'W, 2200 m, *D. S. Barrington* 1215 (VT). **San José:** Quebrada de los Yases, entre Palmilera & San Joaquín de Dota, 1700 m, *A. Jiménez M.* 1475A (CR, F, NY, US). **San José/Cartago:** near El Trinidad & Km. 72 (20 km SE from Empalme) along Interamer. hwy., 9°40'N, 83°53'W, *W. Burger & R. G. Stolze* 5965 (CR, F). PANAMA. **Chiriquí:** Holcomb's trail, 8–10 mi. above El Boquete, Chiriquí, 1400–1550 m, *E. P. Killip* 5059 (US).

3. *Polystichum dubium* (H. Karst.) Diels, *Nat. Pflanzenfam.* [Engler & Prantl] 1(4): 194. 1899. Basionym: *Phegopteris dubia* H. Karst., *Fl. Columb.* (H. Karst.) 1: 169, tab. 84. 1861. *Cyrtomium dubium* (H. Karst.) R. M. Tryon & A. F. Tryon, *Rhodora* 83: 134. 1981. TYPE: Colombia. s.d., *H. Karsten s.n.* (holotype, LE not seen; isotype, B!). Figure 1.

This species is the type of *Polypodium* sect. *Cyrtomiphlebium* Hook., *Sp. Fil.* 5: 15. 1864.

Rhizome erect, ca. 3 cm diam. Fronds typically 25–40 cm, spreading; petiole scales ca. 1 cm, lanceolate, conform, atropurpureous with a narrow ochraceous edge, the edge sharply distinct from the center, petiole-scale cilia short, stiff, infrequent. Laminae ca. 3 times as long as wide, acute, 1-pinnate and irregularly crenate, without a bulbil; pinnae acuminate and falcate, ca. 3 times as long as wide, barely ascendant, inequilateral but without an auricle, spinules absent, the basal pinnae shorter than the next distal; pinna-rachis scales filiform, ochraceous. Indusia absent.

Discussion. *Polystichum dubium* is unique among Costa Rican polystichums in being strictly once-pinnate. It could be taken as a small *Phanerophlebia* C. Presl; it differs from *Phanerophlebia* in being exindusiate with gradually reduced leaf apices instead of indusiate with conform leaf apices. Neither is it a *Cyrtomium*, which in the strict sense is an Old World genus of indusiate *Polystichum* allies with subconform frond apices and multiple stories of areolae.

Polystichum dubium has been collected at two sites in Costa Rica between 1800 and 2500 m, one from Porrosatí on the Pacific slope of Volcán Barba in the Cordillera Central and the other from Coto Brus on the lower Pacific slopes of the Cerro de Talamanca near Panama. Ecologically this species has a strong preference for the earthen banks of streams in lower montane forests. At the lower limit of its elevational distribution, it shares the stream bank habitat with *P. platyphyllum*. Most of the appropriate habitat is now lost to urbanization in the Valle Central, and the species is lost from the Volcán Barba site.

At the northern limit of its distribution in Costa Rica, the species is known in the Andes from Colombia to Bolivia (Kessler et al., 2005), where *Polystichum dubium* has been found much more frequently than in Costa Rica in recent years. There is no cytological information for this species. The lack of a true indusium and the strong presence in the northern and central Andes suggests that *P. dubium* pertains to the Andean clade.

Selected specimens examined. COSTA RICA. **Heredia:** slopes of Barba, Porrosatí, 2500 m, *W. H. Wagner & F. S. Wagner* 79019 (NY); above Porrosatí, slopes of Volcan Barba, 2500 m, *W. H. Wagner & F. S. Wagner* 77503 (US). **Puntarenas:** Coto Brus, Zona Protectora Tablas, Sendero Sur, 1900–2000 m, 8°57'03"N, 82°45'03"W, *A. Rojas & P. L. Pacheco* 5075 (VT).

4. *Polystichum hartwegii* (Klotzsch) Hieron., *Hedwigia* 46: 355. 1907, as “hartwegii.” Basionym: *Aspidium hartwegii* Klotzsch, *Linnaea* 20: 366–367. 1847. TYPE: Guatemala. Las Nubes mtn.,

near Guatemala City, 1839–1840, *K. T. Hartweg* 631 (holotype, B not seen; isotypes, BM!, K!, P not seen). Figure 2.

Polystichum drepanoides E. Fourn., *Mexic. Pl.* 1: 92. 1872. TYPE: Mexico. “inter San Bartolo et Pueblo-Novio,” s.d., *J. J. Linden s.n.* (holotype, P not seen, P photo at US!).

Aspidium trejoi Christ, *Bull. Herb. Boissier*, sér. 2, 5: 255. 1905, as “Trejoi.” TYPE: Mexico. Chiapas: San Pablo, 2000 m, *G. Münch* 167 (lectotype, designated by A. R. Smith [1981: 197], P not seen; isoelectotype, DS!).

Rhizome erect, to at least 4 cm diam. Fronds to 80 cm, spreading; petiole scales ca. 2 cm, narrow-lanceolate, conform, fuscous with a fulvous edge, the edge sharply distinct from the center, petiole-scale cilia short and broad, infrequent. Laminae ca. 3.5 times as long as wide, 2-pinnate and crenate to usually 2-pinnate pinnatifid, acuminate, without a bulbil; pinnae attenuate, ca. 5(to 7) times as long as wide, attached at right angles to the rachis, the basal pinnae barely shorter than the next distal or the same length; pinna-rachis scales filiform, amber; pinnules flat, obliquely attached especially distally, the auricle weakly developed, the apex blunt, spinules well-developed, the basal acroscopic pinnule of the medial pinnae longer than the adjacent pinnule. Indusia 1 mm or more in diam.

Discussion. *Polystichum hartwegii* has a unique combination of large indusia and filiform pinna-rachis scales. There is extensive superficial variation in pinna and pinnule shape and size in *P. hartwegii*, which is one of the reasons for the number of synonyms.

Polystichum hartwegii occurs at 1200–2300 m in lower montane and premontane moist to wet forests and areas cleared from them on the Cordillera de Talamanca. However, there are few recent collections. This species is among the most widely distributed of the New World tropical group, extending from southern Mexico to Bolivia (Kessler et al., 2005). In Guatemala, the species has been encountered at unexpectedly high elevations (up to 2900 m, *T. S. Quedensley* 659, VT!).

The two syntypes of *Aspidium trejoi* that remained after the earlier designation of the lectotype from Mexico (Smith, 1981: 197) are both Costa Rican collections, which pertain to at least three species, only one of which is *Polystichum hartwegii*. I have seen the following: Costa Rica, San José Province, El Copey, Bords du Río Pedregoso, 1800 m, *Tonduz* 11853 (CR! [det. *P. alfaroi*], US 365951!, US 830938! [det. *P. concinnum*]); Copey, *Tonduz* 11894 (CR! [det. *P. hartwegii*]).

Selected specimens examined. COSTA RICA. **Cartago:** mtns. above Tres Ríos, 5000 ft., *E. Scamman & L. R. Holdridge* 7944 (GH, US). **Limón:** Cordillera de Talamanca, Atlantic slope, canyon of Río Siní, 1800–1900 m, 09°13'N, 82°59'W, *G. Davidse & G. Herrera* Ch. 29118 (VT). **San José:** forêts du Copey, 1800 m, *A. Tonduz* 11894 (BM, CR, US).

5. *Polystichum lilianiae* Barrington, *Brittonia* 55: 321, fig. 2. 2003, as “lilianae.” TYPE: Costa Rica. Cartago: Villa Mills, Km. 95 on Pan American Hwy., 3100 m, 15 Jan. 1993, *D. S. Barrington* 2042 (holotype, VT!; isotypes, NY!, UC!). Figure 1.

Rhizome erect, ca. 2 cm diam., supported by adventitious roots. Fronds typically ca. 50 cm, spreading; petiole scales ca. 1 cm, lanceolate, fuscous with a broad stramineous edge, the edge sharply distinct from the center, petiole-scale cilia short, stiff, frequent. Laminae at most 3 times as long as wide, acuminate, 2-pinnate and serrate, without a bulbil; pinnae attenuate, ca. 6 times as long as wide, attached at right angles to the rachis, the basal pinnae the longest; pinna-rachis scales lanceolate, ochraceous; pinnules flat, attached at oblique angles throughout, the auricle weakly developed, the apex acute, spinules well-developed, the basal acroscopic pinnule of the medial pinnae longer than the adjacent pinnule. Indusia ca. 1 mm in diam.

Discussion. *Polystichum lilianiae* is one of two montane rainforest *Polystichum* species in Costa Rica with small leaves and thin rhizomes; the other is *P. turrialbae*. The two are compared below, in the treatment of *P. turrialbae*. *Polystichum lilianiae* sometimes has anomalous foliage, with the pinnules distorted and reduced.

Polystichum lilianiae is endemic to the Cordillera Central and the Cordillera de Talamanca in Costa Rica; it may be expected in contiguous montane regions in Panama. It is occasional in montane rainforests dominated by *Quercus* L. species from 2500 to 3000 m.

Polystichum lilianiae is an allotetraploid with *P. turrialbae* as one of its progenitors (Barrington, 2003). The other progenitor is unknown, but judging from the differences between *P. turrialbae* and *P. lilianiae*, the second progenitor should be a species with dark petiole scales, fairly small (ca. 0.6 mm) indusia, the basal pinnae broadest, and pinnule attachment strongly oblique. Given its morphology, this species appears to be a fertile hybrid combining the heritage of two different species of the Mayan clade.

Selected specimens examined. COSTA RICA. **Cartago:** Villa Mills, S of La Georgina, NNE of hwy. across from first

borrow pit, *D. S. Barrington* 677, 679 (CR, VT); Villa Mills, in dense thicket in oak forest below & just W of Hotel La Georgina at Km. 95 on Pan Amer. Hwy., *D. S. Barrington* 1926 (CR). **Heredia:** NE slope Volcán Barva, betw. Laguna del Barva & base of Caños las Marías, 2450–2800 m, 10°08.5'N, 84°07'W, *M. Grayum* 7455 (CR).

6. *Polystichum muricatum* (L.) Fée, Mém. Foug. 5. Gen. Filic. 278. 1852. Basionym: *Polypodium muricatum* L., Sp. Pl. 2: 1093. 1753. TYPE: tab. 1, fig. 6, Petiver, Pter. Amer. 53. 1712 (lectotype, designated by Proctor [1985: 460, tab. 1, fig. 6], Petiver [1712]). Figure 1.

Aspidium moritzianum Klotzsch, Linnaea 20: 367. 1847. TYPE: Venezuela. Aragua: Colonia Tovar, *J. W. K. Moritz* 280 (holotype, B not seen; isotypes, GH!, K!).

Rhizome ascendant, ca. 2 cm diam. Fronds commonly 60–90 cm, spreading; petiole scales ca. 1 cm, lanceolate, conform, fuscous with a narrow fulvous edge, the boundary between edge and center indistinct, petiole-scale cilia absent. Laminae ca. 4 times as long as wide, acuminate, 2-pinnate pinnatifid, without a bulbil; pinnae attenuate, ca. 5 times as long as wide, attached at right angles to the rachis; the basal pinnae barely if at all shorter than the next distal; pinna-rachis scales linear, fulvous; pinnules flat, attached at right angles throughout, the auricle weakly developed, the apex rotund, spinules well-developed, the basal acroscopic pinnule of the medial pinnae longer than the adjacent pinnule. Indusia ca. 0.3 mm in diam.

Discussion. The combination of very small indusia and petiole scales that totally lack cilia is unique to *Polystichum muricatum*. The relatively thin-textured lamina, the linear pinna-rachis scales, and the unique apex shape of the pinnules (rotund with a well-developed spinule) help in identification as well.

Known from Cerros de la Carpintera, the Cordillera Central, Cerro de Talamanca (Cerros de Escazú region), and the Cordillera de Guanacaste at 1000–2700 m elevation, *Polystichum muricatum* is occasional in intact forests and secondary growth, predominantly in premontane wet forests.

A broad-ranging tropical American species, *Polystichum muricatum* is known throughout Central America (although missing from Guatemala), the Greater Antilles, and from Venezuela (*J. Mostacero et al.* 88, VT!) to Ecuador (*D. S. Barrington* 1062, VT!). This broad concept of *P. muricatum* needs testing with modern genetic tools. The species is diploid, based on counts from Mexico (Mickel et al., 1966; Smith & Mickel, 1977). Phylogenetically, Costa Rican *P. muricatum* is a member of the Mayan clade.

Selected specimens examined. COSTA RICA. **Cartago:** Cerro de la Carpintera, 1500–1850 m, *P. C. Standley* 35767 (US); Cerros de la Carpintera, end near Boy Scout Camp, 9°54'N, 83°59'W, *D. S. Barrington* 1228 (CR); along rd. to Planta Eléctrica María del Rosario, near Río Tiribí, NE of Tres Ríos, 9°57'N, 83°58'W, 1750 m, *M. H. Grayum* & *P. Sleeper* 3308 (MO, UC). **Puntarenas:** Monteverde, beginning of rd. to San Luis, coppice in cow pasture, 1450 m, *D. P. Little* & *D. S. Barrington* 349 (VT). **San José:** Cerro de Piedra Blanca, above Escazú, *P. C. Standley* 32511 (US).

7. *Polystichum nudicaule* Rosenst., Repert. Spec. Nov. Regni Veg. 11: 56. 1912. TYPE: Bolivia. Nor Yungas: “Yungas septentrionalis,” Unduavi, 3400 m, *O. Buchtien* 2658 (lectotype, designated here, US!; isolectotype, UC!). Figure 2.

Rhizome erect, ca. 1 cm diam. *Fronds* to 45 cm, spreading (erect in full sun). Petiole scales ca. 1.5 cm, broad-lanceolate, conform, atropurpureous, petiole-scale cilia both short and stiff and long and delicate, frequent distally on the scales. Laminae 2 to 3 times as long as wide, long-attenuate, 2-pinnate and crenate, without a bulbil. Pinnae attenuate, ca. 5 times as long as wide, attached at right angles to the rachis; the basal pinnae as long as or longer than the more distal. Pinna-rachis scales long-lanceolate, ferruginous. Pinnules revolute (flat in deep shade), attached at slightly oblique angles throughout, the auricle poorly developed, the apex acute, spinules weak (irregularly developed), the basal acroscopic pinnule of the medial pinnae barely longer than the adjacent pinnule. Indusia absent.

Discussion. *Polystichum nudicaule* in Costa Rica is a páramo *Polystichum* with long-attenuate blades that are broadest at the base and pinnules that are attached to the pinna-rachis at a slightly oblique angle. In addition, the rachis has many more narrow-lanceolate, atropurpureous scales than *P. talamancanum*, a frequent companion in the páramo. The pinnules are strongly revolute in sun but flat in shaded locations (Barrington, pers. obs.).

Polystichum nudicaule has been found so far in Costa Rica only on the Cerro de la Muerte, Cordillera de Talamanca, at ca. 3400 m, but it is to be expected in the high páramos of the Chirripó massif. At the Cerro de la Muerte it grows above treeline in sheltered areas, both in stream beds and among páramo shrubs and treelets, where the taxon may be easily overlooked as it resembles *P. talamancanum* juveniles, which differ in their narrow-based blades with acute or at most short-attenuate tips. The extreme forms with small leaves and revolute pinnules resembling the Bolivian lectotype of *P. nudicaule* are found among páramo vegetation in full sun.

Polystichum nudicaule is found from Costa Rica to Bolivia (Kessler et al., 2005). In the Central Andes it is common in high-elevation forests and páramos. Ploidy is unknown. It is probably a member of the Andean clade—since it is exindusiate, it is in the same clade as the Central Andean *P. montevidense* (Spreng.) Rosenst. in molecular analysis (Driscoll & Barrington, 2007)—and it is found only in Costa Rica outside the Central Andes. In my previous work, I included *P. nudicaule* in a broadly defined *P. lehmannii* Hieron., but the two are distinct enough to merit recognition as separate species, following Kessler et al. (2005). *Polystichum lehmannii* has spinules well-developed on the pinnules, not confined to auricle and apex or absent. In addition, *P. lehmannii* has pinna-rachis scales with a yellow hue (they are amber to fulvous), whereas *P. nudicaule* has pinna-rachis scales with a reddish hue (they are typically ferrugineous in Costa Rica).

Remaining syntypes are also from the type locality in Bolivia and include three other collections by Buchtien: *O. Buchtien* 2657 (syntype, B not seen; isosyntype, US!), *O. Buchtien* 2659 (isosyntype, US!), *O. Buchtien* 2662 (not seen).

Selected specimens examined. COSTA RICA. **San José:** Cordillera de Talamanca, Buenavista-Massiv, Cerro Páramo, Westhang, 3275 m, *H. Kuhbier* & *L. D. Gómez* *P.* 298 (CR); SE of towers, Cerro de la Muerte, *D. S. Barrington* 975 (VT); shady niches on wall of deep stream course cut into páramo, area of transmission towers, Cerro de la Muerte, *D. S. Barrington* 1964 (CR); area of towers at summit of Cerro de la Muerte, 3400 m, *D. S. Barrington* 2137 (VT).

8. *Polystichum orbiculatum* (Desv.) J. Rémy & Fée, *Fl. Chil.* [Gay] 6: 515. 1853. Basionym: *Aspidium orbiculatum* Desv., *Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin* 5: 321. 1811. TYPE: “in America australi,” [*A. N. Desvaux s.n.*] (holotype, P!). Figure 2.

Nephrodium polyphyllum C. Presl, *Reliq. Haenk.* 1: 37. 1825. TYPE: “Habitat in Peruvia? In Chile?,” *T. Haenke s.n.* (holotype, PR!).

Nephrodium trapezoides C. Presl, *Reliq. Haenk.* 1: 37. 1825, non *Polystichum trapezoides* (Sw.) C. Presl, *Tent. Pterid.* 83. 1836. TYPE: Peru. “in montanis Peruviae,” *T. Haenke s.n.* (holotype, PR not seen; isotype, K!).

Polypodium rigidum Hook. & Grev., *Icon. Filic.* 2: t. 163. 1831. TYPE: Peru. “Ad verticum montis Pichincha,” *W. Jameson s.n.* (holotype, K!), non *P. rigidum* Aubl., *Hist. Pl. Guiane* 2: 963. 1775.

Polypodium saxatile Klotzsch, *Linnaea* 20: 383. 1847. TYPE. Peru. “[A]d Diezmo in locis umbrosis, saxosis,” *H. Ruiz L.* 65 (holotype, B!).

Polystichum pumilio Maxon, *J. Wash. Acad. Sci.* 19: 197, fig. 1. 1929. TYPE: Ecuador. Chimborazo: Urbina,

3475 m, 22–28 Oct. 1923, *H. E. Anthony* & *G. H. H. Tate* 394 (holotype, US-01424988!). [The species epithet, a noun in apposition, should stand as originally coined.]

Polystichum pygmaeum Copel., *Univ. Calif. Publ. Bot.* 19: 300, tab. 56. 1941. TYPE: Bolivia. [La Paz:] 13 km S of Tiahuanaco, 4200 m, 31 Mar. 1936, *J. West UC Exped.* 6393 (holotype, UC-602775!).

Rhizome erect, ca. 3 cm diam. Fronds to 65 cm, stiffly erect; petiole scales ca. 1 cm, broad-lanceolate, conform, rufous, petiole-scale cilia long and delicate, frequent. Laminae ca. 9 times as long as wide, attenuate, 2-pinnate and crenate (basal pinnules of the pinnae sometimes pinnatisect), without a bulbil; pinnae acute, ca. 6 times as long as wide, strongly ascendant except in shade; the basal pinnae longer than the next distal. Pinna-rachis scales lanceolate, rufous; pinnules strongly revolute except in shade, attached at right angles throughout, the auricle weakly developed, the apex blunt, spinules weak (the pinnule apex without a single well-developed spinule), the basal acroscopic pinnule of the medial pinnae longer than the adjacent pinnule. Indusia absent.

Discussion. *Polystichum orbiculatum* is a páramo species with extremely narrow leaves, strongly ascendant pinnae, and rufous scales. Above treeline in Costa Rica, there are two stiffly erect, twice-pinnate polystichums that routinely grow in full sun, *P. orbiculatum* and *P. talamancanum*. The latter is much more common and differs in having fuscous petiole scales, longer pinnae, and pinnules with a strong apical spinule. *Polystichum orbiculatum* varies remarkably with habitat; shade forms are flat and lax while sun forms are rigidly erect with strongly revolute pinnules. High-elevation individuals are dwarfed as well. This variation explains the large number of names that have been coined for the species.

In Costa Rica, *Polystichum orbiculatum* is known only from the Cerro de Talamanca, where it grows in páramos and open, disturbed areas from 3100 to 3800 m. While this species is only rarely found below 3400 m, in contrast, the similar *P. talamancanum* descends below treeline to ca. 3000 m on road cuts.

Polystichum orbiculatum s.l. is widespread in tropical America, collected from Mexico (Mickel & Smith, 2004) to Bolivia (Kessler et al., 2005); it is absent in the West Indies. It is a tetraploid species based on counts from Costa Rica (Barrington, 1990), but small-spored individuals from the northern Andes suggest that the taxon in the broad sense as here construed includes at least one of its progenitors (Barrington et al., 1986).

Selected specimens examined. COSTA RICA. **San José:** summit of Cerro de la Muerte, S side of northern-most

summit with radio towers, 9°33'34"N, 83°45'13.5"W, *D. S. Barrington 1284* (CR); trail Valle de los Leones, lower part of Valle de los Conejos, Río Talari [Cerro Chirripó], 9°27'N, 83°31'W, 3400 m, *W. C. Burger & L. D. Gómez P. 8308* (F, NY); Cerro Chirripó massif; area betw. Refugio & lake at head of Río Dikebi, 3500 m, *G. Davidse & R. W. Pohl 1548* (MO); Cerro de la Muerte, Cordillera de Talamanca; 3100–3400 m, *A. F. Skutch & M. Barrantes 5192* (MO).

9. *Polystichum platyphyllum* (Willd.) C. Presl, Tent. Pterid. 84. 1836. Basionym: *Aspidium platyphyllum* Willd., Sp. Pl., ed. 4 [Willdenow] 5(1): 255. 1810. TYPE: Venezuela. "Habitat ad Caracas in montosis nemorosis," *F. Bredemeyer s.n.* (holotype, B-W 19789!). Figure 1.

Polystichum opacum Rosenst., Hedwigia 46: 112. 1906. TYPE. Brazil. Rio Grande do Sul: Mun. Rio Pardo, Fazenda Soledade, 1904, *C. Jürgens 42* (lectotype, designated here, B not seen; isoelectotypes, NY!, UC 441761!).

Rhizome ascendant, ca. 2 cm diam., supported by adventitious roots. Fronds to 60 cm, wide-spreading; petiole scales ca. 1 cm, lanceolate, conform, fulvous to stramineous, petiole-scale cilia short. Laminae ca. 2.5 times as long as wide, long-attenuate, 2-pinnate and crenate, with a subapical bulbil; pinnae acuminate, ca. 4 times as long as wide, attached at right angles to the rachis; the basal pinnae about the same length as the next distal. Pinna-rachis scales filiform, fulvous; pinnules flat, attached at slightly oblique angles throughout, the auricle weakly developed, the apex blunt, spinules weak (developed only at apex and auricle), the basal acroscopic pinnule of the medial pinnae longer than the adjacent pinnule. Indusia absent.

Discussion. *Polystichum platyphyllum* is unmistakable: even when the subapical leaf bulbil is missing, the long-attenuate, once-pinnate leaf apex is unique among Costa Rican polystichums. In addition, the other twice-pinnate polystichums from middle and lower elevations are all indusiate. In living plants, the leaf apex, from the area of the bulbil distally, is bent so that it is parallel to the ground. In the field, the leaves have a lustrous green texture above. As the name implies, the pinnules are consistently flat, never recurved at all.

This species is known from the Cordillera de Tilarán, the Cordillera Central, and the Cordillera de Talamanca at elevations from 600 to 1500 m. This is the lowest elevation preference of any *Polystichum* in Costa Rica. *Polystichum platyphyllum* characteristically grows on soil banks in premontane wet and rainforests; these soil banks are usually near streams, and the plants are often encountered directly over flowing water. This habitat preference is shared only

with the once-pinnate and bulbless *P. dubium* in Costa Rica. *Polystichum platyphyllum* is not commonly encountered in Costa Rica; a number of historical localities (e.g., on the Río Torres in San José) have been destroyed by human activity.

Polystichum platyphyllum is perhaps the most widely distributed *Polystichum* species in tropical America: it is known from Mexico (*D. S. Barrington 2029*, VT!) to Bolivia (*P. G. Windisch 2373*, VT!) as well as Brazil and Argentina (*E. R. de la Sota 4076*, US!), and it is also found in the West Indies (Mickel, 1997). Perhaps the taxon's preference for lower-elevation stream banks explains its wide distribution. Its closest allies are probably among species of the Andean clade, since it is sister to the Central Andean *P. montevidense* in molecular analysis (Driscoll & Barrington, 2007) and lacks an indusium. *Polystichum platyphyllum* is diploid, based on a count from Mexico (Smith & Mickel, 1977).

Remaining syntypes of *Polystichum opacum* are from the type locality in Rio Grande do Sul and include two other Jürgens collections: *C. Jürgens 71* (B not seen); 1 Sep. 1904, *Jürgens 235* (B not seen; isosyntype, UC 441760!).

Selected specimens examined. COSTA RICA. **Alajuela:** alrededores de San Ramón, NO lado, *A. M. Brenes 15320, 15341* (CR). **Heredia:** Barba, foot of Volcán Barba, 1100 m, *E. Scamman 7082* (GH, US). **Puntarenas:** Sierra de Tilarán, Monteverde, *C. W. Palmer 154* (CR, NY). **San José:** Finca Fortuna, Desamparados, 3800 ft., *E. Scamman & L. R. Holdridge 7943* (GH, US); basin of El General, 675–900 m, *A. F. Skutch 5207* (MO, NY, UC).

10. *Polystichum speciosissimum* (A. Braun ex Kunze) R. M. Tryon & A. F. Tryon, Rhodora 83: 136. 1981. Basionym: *Cheilanthes speciosissima* A. Braun ex Kunze, Analecta Pteridogr. 35, tab. 23. 1837. *Plecosorus mexicanus* Fée, Mém. Foug., 5 Gen. Fil. 150, pl. 13A, fig. 1. 1852, nom. superfl. *Plecosorus speciosissimus* (A. Braun ex Kunze) T. Moore, Index Fil. [T. Moore], xl. 1857. TYPE: Mexico, Sep. 1827, *W. F. Karwinski* (holotype, LZ not seen; isotype, B!). Figure 2.

This species is the type of the genus *Plecosorus* Fée, Mém. Foug., 5 Gen. Fil. 150, Pl. 13, 1850–1852.

Plecosorus mexicanus is a renaming of *Cheilanthes speciosissima*, based on the type of that name.

Rhizome erect, ca. 8 cm diam. Fronds to 90 cm, erect-ascending; petiole scales ca. 2.5 cm, long-lanceolate, conform, orange, petiole-scale cilia mostly short and broad (some long and delicate). Laminae 3 to 4 times as long as wide, acuminate, 2-pinnate pinnatisect, without a bulbil; pinnae attenuate, ca.

4.5 times as long as wide, attached at right angles to the rachis; the basal pinnae barely shorter than the next distal; pinna-rachis scales narrow-lanceolate, rufous; pinnules strongly revolute, attached at right angles throughout, the auricle weakly developed, the apex blunt, spinules absent (pinnule margins lacerate, scarious), the basal acroscopic pinnule of the medial pinnae longer than the adjacent pinnule. Indusia absent (false indusium present).

Discussion. The unmistakable *Polystichum speciosissimum* is one of the showpieces of the Costa Rican páramo. The highly dissected leaves, unusually pale for *Polystichum*, form a steeply ascending rosette approaching a meter high, and the mass of brilliant orange scales at the petiole bases is unique. The undersides of the young leaves are also covered with orange scales; these fade to white with age. The pinnae are often curved downward in the plane of the leaf toward the ground. Old individuals build thick trunks some 20 cm high. *Polystichum speciosissimum* has a discrete hyaline edge to the ultimate segments; that is, it has a false indusium reminiscent of the Pteridaceae, hence its taxonomic inauguration in *Cheilanthes* Sw.

Restricted to páramos in Costa Rica, *Polystichum speciosissimum* is found in the Cerro de Talamanca, including the Cerro de la Muerte and Cerro Chirripó, from 3100 to 3800 m. This species often has brown necrotic areas on the leaves, apparently the result of frost damage.

Polystichum speciosissimum has a disjunct distribution between the Sierra Talamanca and the mountains of Mexico and Guatemala (documented for the latter by Stolze [1981]). Isozyme data reveal the Costa Rican populations to be a genetically depauperate subset of those in northern Mesoamerica, suggesting recent dispersal from north to south (Barrington, 2005). It is diploid, based on counts from Costa Rica (Barrington, 1990). *Polystichum speciosissimum* is sister to the remainder of the continental tropical American polystichums so far analyzed, suggesting that it originated early in the history of the Neotropical clade (Driscoll & Barrington, 2007). Its geography points to a northern origin for the clade. As it is deeply nested within *Polystichum* (Driscoll & Barrington, 2007), there is no basis for recognizing *P. speciosissimum* as a separate genus, in spite of its distinctive morphology.

Selected specimens examined. COSTA RICA. **Cartago:** Cerro de la Muerte, roadcut N side of Pan American Hwy. betw. high point in rd. & first dwellings, ca. 3300 m, *D. S. Barrington 812a* (VT). **San José:** area of towers at summit of Cerro de la Muerte, 3400 m, *D. S. Barrington 2149* (CR); same locality, *D. S. Barrington 2150* (VT).

11. *Polystichum talamancanum* Barrington, Ann. Missouri Bot. Gard. 76: 369, f. 2. 1989. TYPE: Costa Rica. Cartago: highest point on Pan-American Hwy., Cerro de la Muerte, 3330 m, 4 Jan. 1980, *D. S. Barrington 708* (holotype, GH!; isotypes, CR!, VT!). Figure 2.

Rhizome erect, ca. 8 cm diam. Fronds to 100 cm, stiffly erect; petiole scales ca. 1.5 cm, long-lanceolate, conform, fuscous, petiole-scale cilia both short and stiff and long and delicate. Laminae ca. 5 times as long as wide, acuminate to attenuate, 2-pinnate and serrate, without a bulbil; pinnae acuminate (to attenuate), 4 to 5 times as long as wide, strongly ascendant; the basal pinnae at least as long as the next distal; pinna-rachis scales narrow-lanceolate, fulvous to ochraceous; pinnules strongly revolute, attached at right angles throughout, the auricle prominent, the apex acute, spinules well-developed (pinnule apex with a single well-developed spinule), the basal acroscopic pinnule of the medial pinnae longer than the adjacent pinnule. Indusia absent (occasionally weakly developed proximally on the pinnae).

Discussion. In its typical habitat on open páramo, *Polystichum talamancanum* is a stiffly erect *Polystichum* with dark, long-ciliate petiole scales and pointed, revolute pinnules. Rarely, it has partially developed indusia, especially on the pinnules nearest the rachis. This species also grows in shady sites above treeline, where the pinnules are nearly flat. These shade-form plants are easily confused with the much less common *P. nudicaule*, where they grow together; *P. talamancanum* differs in having blades that are broadest above the base and pinnules attached at right angles to the pinna-rachis. *Polystichum talamancanum* is notable for precociously fertile individuals, including *Barrington 583* (CR), which has a fertile lamina only 15 cm long.

Polystichum talamancanum is a common and prominent plant of the Cordillera de Talamanca, where it grows in páramos and in disturbed sites in the montane rainforests from 3000 to 3400 m. It is the most tolerant of high insolation and cold of the polystichums, judging from the frequency and excellent condition of the plants in exposed, apparently high-water-stress sites in the páramo. I have seen hummingbirds gathering rachis scales from this species, presumably to line their nests.

Endemic to Costa Rica and Panama, this allotetraploid (Barrington, 1990) apparently originated recently in these mountains. One progenitor is the endemic *Polystichum concinnum*; another is an unknown taxon also involved in the origin of *P.*

orbiculatum (Barrington, 1990). It seems likely that this species is unique in combining the genetic heritage of the Mayan clade and Andean clade.

Selected specimens examined. COSTA RICA. **Cartago:** Villa Mills, 1.0 km N of Restaurant La Georgina, *D. S. Barrington* 577 [shade form] (CR). **Limón:** Cordillera de Talamanca, peak of Cerro Kámuk, 9°16'30"N, 83°02'W, 3350–3549 m, *G. Davidse* 26008 (CR, MO). **San José:** Cerro de la Muerte, summit of Cerro de la Muerte, "ox-trail," off side of rd. to transmission towers, *D. S. Barrington* 1285 (CR). **San José/Cartago:** Cerro de la Muerte, roadcut; vertical rockface, *D. S. Barrington* 583 (CR); páramo region, Cerro de la Muerte, Cordillera de Talamanca, 3100 m, *L. O. Williams* 24476 (F, NY, US); Cerro Chirripó, SW slopes, along trail from Canaán to summit, near la caverna, 9800–10,300 ft., *A. M. Evans, D. B. Lellinger & F. Bowers* 110 (MO, US).

12. *Polystichum turrialbae* Christ, Bull. Herb. Boissier, sér. 2, 6: 163. 1906. TYPE: Costa Rica. Heredia: Volcán Turrialba, 1905, *K. Wercklé s.n.* (holotype, P!). Figure 1.

Polystichum smithii Mickel & Beitel, Mem. New York Bot. Gard. 46: 315. 1988. TYPE: Mexico. Oaxaca: summit of Cerro San Felipe, 18 km N of Rte. 175, 9500 ft., *J. T. Mickel* 7056 (holotype, NY!).

Rhizome erect, ca. 2 cm diam., supported by adventitious roots. Fronds typically ca. 60 cm but reaching 90 cm, spreading; petiole scales ca. 1 cm, lanceolate, conform, stramineous or stramineous with a weakly developed fulvous center, the boundary between edge and center indistinct, petiole-scale cilia short, stiff, frequent. Laminae about twice as long as wide, acuminate, 2-pinnate and serrate, without a bulbil; pinnae acuminate, ca. 6 times as long as wide, attached at right angles to the rachis; the basal pinnae shorter than the next distal; pinna-rachis scales long-lanceolate, ochraceous; pinnules flat, attached at right angles throughout, the auricle poorly developed, the apex acute, spinules well-developed, the basal acroscopic pinnule of the medial pinnae longer to much longer than the adjacent pinnule. Indusia over 1 mm in diam.

Discussion. *Polystichum turrialbae* is one of two high-montane forest *Polystichum* species in Costa Rica with small leaves and thin rhizomes; the other is *P. lillianiae*. In both species, the rhizomes are erect-ascending and supported by adventitious roots. The leaves of *P. turrialbae* are less lustrous than those of *P. lillianiae*, and the basal pinnae are shorter than the next distal pair rather than longer. The petiole scales without a sharply demarcated central dark stripe also distinguish this species from *P. lillianiae*. The similar *P. fournieri* A. R. Sm. is endemic to montane rainforests of southern Mexico and western Guate-

mala. Formerly, the name *P. fournieri* was used for all of these species, including all Costa Rican plants, so the name is common on Costa Rican specimens but never (so far) correct. One feature distinguishing both of the species in Costa Rica from the Mexican *P. fournieri* is the droop-tip versus regularly uncoiling veneration, respectively, of the two.

Polystichum turrialbae is a fairly common species growing at 2700–3200 m in oak forests of the Cordillera Central and the Cordillera de Talamanca in Costa Rica. The species is widely distributed from Mexico (Barrington, 1995; Mickel & Smith, 2004) to Bolivia (Kessler et al., 2005). *Polystichum turrialbae* is diploid (Barrington, 2003); it is likely to lie in the indusiate Mayan clade based on its morphology.

Selected specimens examined. COSTA RICA. **Cartago:** Fila Div., Cuericí, 2800 m, *L. D. Gómez P.* 2378 (DS, F, GH, NY, US). **Heredia:** N of Heredia, ca. 1 km beyond Porrosatí, in ravine, 2100 m, *D. B. Lellinger & J. J. White III* 1680 (F, US). **Limón:** Cordillera de Talamanca, headwaters of unnamed W branch of Río Teribe, betw. Río Sini & continental divide at Cerro Bekom, 9°10'45"N, 83°03'30"W, 2500–2600 m, *G. Davidse, G. Herrera Ch. & R. H. Warner* 25740 (CR), 25761 (CR, UC). **San José:** Villa Mills, S of Pan American Hwy. about 1 km E of Hotel La Georgina, *D. S. Barrington* 696 (CR).

HYBRIDS

Polystichum concinnum Lellinger ex Barrington × ***P. speciosissimum*** (A. Braun ex Kunze) R. M. Tryon & A. F. Tryon.

This hybrid is fairly common above treeline on the Cerro de Talamanca in Costa Rica; I have encountered it repeatedly on Cerro de la Muerte. It combines the pale green lamina and paler indument of *Polystichum speciosissimum* with the less dissected lamina of *P. concinnum*; it is at least somewhat revolute. *Barrington* 705 (VT), the first documented plant of this hybrid, was a large plant when I first collected material from it in 1979, and it remains alive and prosperous as of 2011, having attained an age of at least 32 years.

Selected specimens examined. COSTA RICA. **Cartago:** Cerro de la Muerte, roadcut on Pan American Hwy. near treeline, *D. S. Barrington* 705 (CR, VT). **San José:** Cerro de la Muerte, summit with radio towers, 3400 m, 9°33.5'N, 83°45.2'W, *D. S. Barrington* 1274 (VT).

Polystichum concinnum Lellinger ex Barrington × ***P. talamancanum*** Barrington

This is the commonest of the hybrids encountered in Costa Rica. It is regularly found between 3000 and 3400 m along the Pan American Highway on the Cerro de la Muerte. The pinnae are ascendant like

Polystichum talamancanum but barely revolute and much longer. The true indusia are better developed than in *P. talamancanum*, though still variously vestigial (see Barrington, 1985).

Selected specimens examined. COSTA RICA. **Cartago:** Villa Mills, 0.5 km N of Restaurant La Georgina, 3200 m, *D. S. Barrington 574* (CR, VT). **San José:** Talamanca Range, Rte. 2, Villa Mills, 0–1 km NW of Restaurant La Georgina, Km. 95, 3100–3200 m, *S. R. Hill 17521* (VT).

***Polystichum orbiculatum* (Desv.) J. Rémy & Fée × *P. talamancanum* Barrington**

Documented once using cytology and isozymes (Barrington, 1990), this hybrid strongly resembles *Polystichum orbiculatum*, but its pinnules are acuminate with a single strong spinule at the tip, as in *P. talamancanum*.

Specimen examined. **San José:** Cerro de la Muerte, S side of N summit with radio towers, 9°33'34"N, 83°45'13.5"W, *D. S. Barrington 1283* (GH, VT).

***Polystichum speciosissimum* (A. Braun ex Kunze) R. M. Tryon & A. F. Tryon × *P. talamancanum* Barrington**

Documented twice (Barrington, 1990), this hybrid, from above treeline on the Cerro de la Muerte, combines the greater pinnule dissection of *Polystichum speciosissimum* with the strongly spinulose pinnule margins of *P. talamancanum*. Petiole scale hue is intermediate between the progenitors, and pinna-rachis scale hue is pale, favoring *P. speciosissimum*. The heritage of the cited specimens was documented with cytological and isozyme work (Barrington, 1990).

Specimens examined. COSTA RICA. **San José:** SE slope of highest peak of Cerro de la Muerte, *D. S. Barrington 973* (VT); Cerro de la Muerte, S side of N summit with radio towers, *D. S. Barrington 1500* (VT).

SPECIES EXCLUDED FROM COSTA RICA

***Polystichum aculeatum* (L.) Roth, Tent. Fl. Germ. 3(1): 79. 1799. Basionym: *Polypodium aculeatum* L., Sp. Pl. 2: 1090. 1753. TYPE: “Habitat in Europa” (lectotype, designated by Alston [1940: 164], *A. van Royen s.n.*, L [Herb. L.B. 908.311–72] not seen).**

The name *Polystichum aculeatum* was applied by Carl Christensen (Christensen, 1905–1906) to a broad array of twice-pinnate *Polystichum* species from throughout the world, which he reduced to varietal status. However, *P. aculeatum* is currently construed as an allotetraploid species confined to

Europe (Tutin et al., 1993). It combines the features of its diploid progenitors *P. lonchitis* and *P. setiferum* (Forssk.) Moore ex Woynar; none of these plants grows in tropical America.

***Polystichum fournieri* A. R. Sm., Amer. Fern J. 70: 27. 1980. Replaced name: *Polystichum muelleri* Mett. ex E. Fourn. Mexic. Pl. 1: 91.1872, non *Polystichum muelleri* Schumacher, 1803. TYPE: Mexico. Chiapas: forêts des pins, *J. J. Linden s.n.* (lectotype, designated by A. R. Smith [1980: 27], P!).**

This name has been applied to an array of small polystichums from high elevations in Costa Rica. These plants are mostly *Polystichum lilianiae* and *P. turrialbae*. *Polystichum fournieri* is endemic to northern Central America and Mexico (Barrington, 2003).

***Polystichum lehmannii* Hieron., Bot. Jahrb. Syst. 34: 452. 1904. TYPE: Colombia. Depto. Cauca: near Los Motilones, Mt. Sotará, 3000 m, *F. C. Lehmann 3674* (holotype, B!; isotype, US!).**

This name applies to plants from Andean South America.

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